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MARINE PHYTOPLANKTON IN THE REGION OF LA JOLLA, CALIFORNIA, DURING THE SUMMER OF 1924

BY

GEORGE F. SLEGGS

BULLETIN OF THE SCRIPPS INSTITUTION OF OCEANOGRAPHY
LA JOLLA, CALIFORNIA

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INTRODUCTION

From May 17 to October 8, 1924, a series of some three hundred twenty plankton hauls was made in local waters, using the *Sturges*. Figure 1 shows the positions of the various stations where the plankton catches were taken. Most of the collecting was done at

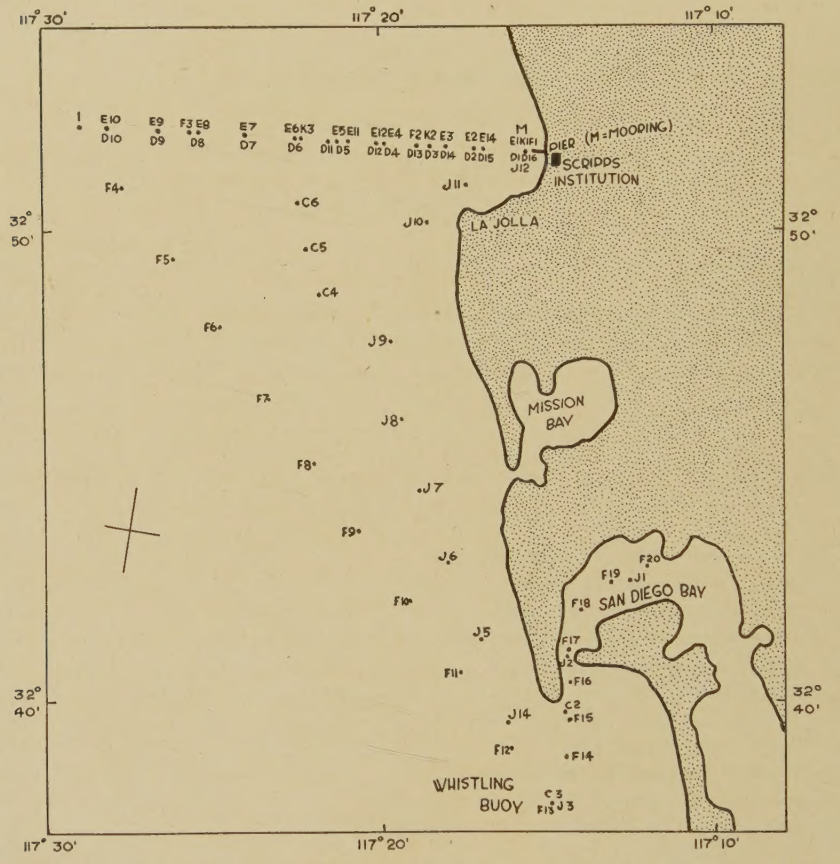

Fig. 1. Map of the area in which the hauls were made, indicating the positions of the stations. From pier to station 1 equals ten miles. Stippled areas indicate sandbars.

established stations 1 and 2, respectively ten and five miles west of the Institution. In all cases a five-gallon sample of sea water was filtered through a small net of No. 25 silk bolting cloth, and the numbers of diatoms and dinoflagellates were ascertained by the method of micro-enumeration. Up to June 27 all catches were made at the surface, but after that date samples were also obtained from

accurately known depths down to sixty meters, by means of the Kofoid self-closing bucket. Concomitantly with the plankton collecting, temperature observations were made, and samples of water were taken for physical and chemical analysis. The work was a continuation of that done in the three preceding years in the La Jolla region.

GENERAL DISCUSSION

Previous analyses (Allen, 1923; Dorman, 1927) have presented evidence in favor of the conclusion that the five-mile station is more productive than the ten-mile one, the interpretation being that proximity to land is associated with a greater amount of land-derived materials which can serve as sustenance for the growth of phytoplankton. The results of the present work, upon the material taken in 1924, bear out this conclusion for the surface level and for the level ten meters below the surface. At the twenty-meter level the productivity was found to be about equal for both stations, while below this depth it turned in favor of the ten-mile station. To make the comparisons, average numbers of cells per liter were calculated for each depth at each station. To obtain averages which would justify a comparison, it was not, of course, legitimate to average all the hauls made in one station-depth unless the distribution of the hauls over the period of time was identical with that at the other station-depth to be compared. For example, as will be seen from the graphs (figs. 2 and 3), many more hauls were made at station 2, surface, than at station 1, surface, during the period of high production of June 8–13, which, if all were taken into account, irrespective of dates, at station 1, would raise unduly the average for station 2. Hence hauls at one station-depth which have no counterpart on the same date at the other station-depth are not taken into account in compiling the averages.

The most extensive comparison was possible in the case of the catches taken at the surface, there being in all fifty-four days on which surface catches were made at both stations within a few hours of each other. While the method of using, as an index of productivity, the number of cells comprised in many different species, of varying size, is not without objections, it has been generally adopted. The results in this paper have been checked by a numerical examination and discussion of the most prominent species individually, and it would appear that the comprehensive totals of all forms can be used in most cases (though not all) as a fairly reliable coefficient of productivity. Taking then the total numbers of cells per liter, we find that the

surface layers at station 2 were markedly more productive than those at station 1, the difference being even more marked than was found by Allen for the same stations in 1922. The averages for the period at station 1 are: diatoms, 13,292; dinoflagellates, 1,832. The averages at station 2 are: diatoms, 19,336; dinoflagellates, 9,913. The greater productivity at station 2 is further borne out by the consistency of the occurrence there of larger hauls than at station 1, on the same days; that is to say, the higher averages are not merely results from a few heavy catches at station 2 among a series otherwise comparable with station 1. Thus, out of 108 comparisons possible between the totals of diatoms and dinoflagellates we find that station 2 exceeded station 1 in 72 instances. Subdividing the period of time we find the differences consistently maintained. The averages are as follows. Through May and June: station 1, 27,165 diatoms, 3,479 dinoflagellates; station 2, 39,509 and 18,173; through July and August, 171 diatoms and 397 dinoflagellates at station 1 as against 244 and 2,716, respectively, at station 2; over September and October, 1,288 diatoms and 317 dinoflagellates at station 1 as against 2,212 and 537, respectively, at station 2.

The comparisons at depths below the surface can hardly be so well established as at the surface owing to the fact that the number of catches made with the Kofoid bucket was limited for each level, the operation taking time, whereas in the case of a surface sample all that is necessary is to lower a pail over the side of the ship. On ten dates hauls were taken at a depth of ten meters at both stations. The averages obtained were: station 1, 291 diatoms and 96 dinoflagellates; station 2, 4,222 diatoms and 277 dinoflagellates. Thus station 2 was again more productive than station 1. It was found, however, that the average for station 2 was raised over 3,000 in the case of diatoms by a pulse of *Dactyliosolen tenuis* Cleve on July 12. Apart from this pulse the productivity of diatoms was about the same. The increase in this species was strongly marked at station 2, reaching its maximum there on July 12. At station 1 it reached its maximum (in the records) two days later, on July 14, though the condition at station 1 on July 13, on which no hauls were taken, is open to conjecture. Since the numbers of this form fell off sharply from July 12 to 14 at station 2, it is possible that the rather small maximum recorded for station 1 may have been preceded by a stronger pulse on July 13. If that had been the case, the productivity for station 1 at 10 meters would have been much greater than shown by the catches, taken as they were at considerable intervals.

Turning now to the records for the twenty-meter depth, we find that, to judge from the averages of sixteen pairs of catches, the greater

productivity of the five-mile station is no longer apparent, there being no significant differences between the average numbers at the two stations. The average numbers are as follows: station 1, 11,118 diatoms and 471 dinoflagellates; station 2, 11,085 diatoms and 422 dinoflagellates.

For the thirty-meter depth fifteen pairs of catches were compared. It is now to be observed that a reversal in productivity is shown, station 1 having a greater amount of phytoplankton. Averages: station 1, 80,231 diatoms, 1,303 dinoflagellates; station 2, 64,109 diatoms and 529 dinoflagellates.

At forty meters we find that the progressive reversal of preponderance is continued. The figures are (based upon eleven catches from each station) : station 1, 62,755 diatoms, 440 dinoflagellates; station 2, 24,906 diatoms and 374 dinoflagellates.

At fifty meters station 1 is still more in excess over station 2. Eight hauls furnished the following averages: station 1, 115,480 diatoms, 675 dinoflagellates; station 2, 32,545 diatoms and 164 dinoflagellates.

At sixty meters only five pairs of catches were available and, taking the averages of these, we find that station 2 is more productive. Averages: station 1, 18,866 diatoms, 140 dinoflagellates; station 2, 27,954 diatoms and 62 dinoflagellates.

It would thus appear that the conditions in 1924 resemble those for some previous years as regards surface production but differ in the relative productivity of the deeper water at points five and ten miles from shore. The contrast between the two stations is more marked at the surface, less marked at a moderate depth, and reversed at a greater depth. If such water could be stirred up somewhat from top to bottom it is evident that the tendency to approach the conditions of former years would appear. At one station there is proportionately more phytoplankton near the surface and less in the lower layers; at the other station there is less at the surface and more in the lower layers. The possibility therefore suggested itself that the differences in distribution of the plankton between 1922 and 1924 might be accounted for by mechanical factors bearing upon the local coastal waters. A considerable body of data being at hand upon surface temperatures and their bearing upon upwelling, I have examined these to ascertain whether the physical conditions of the two years were marked by any noticeable differences. The temperatures at the surface in 1924 were somewhat lower than the average during the summer months, and decidedly less than in 1922. Since low surface temperatures are regarded by McEwen as indicative of a great amount of upwelling of low-level oceanic water, it would appear

that 1924 was more subject to upwelling than 1922, which, if we are to regard upwelling as a factor tending toward greater commingling of the upper layers, appears to be contradictory to the idea of a stratification in the conditions. But it is very doubtful whether in any case so gross a process as the upwelling of oceanic water on an immense scale, such as occurs every year off the coast of California, could have effects upon so localized a process as the degree of commingling of the upper levels. Probably we are faced by factors of greater complexity. The explanation of the differences, which is suggested in this paper, has to do with the character of the plankton in its relation to environmental conditions. The plankton in 1924 appears to have differed very considerably from that described by Allen for 1922 in that the dominant form from the subsurface depths was the oceanic *Rhizosolenia semispina* Hensen. This was more or less constantly associated with other boreal arctic oceanic forms, notably *Chaetoceras criophilum* Castracane and *Thalassiothrix longissima* Cleve and Grunow. The character of the plankton in 1924 seems to have been more oceanic and less neritic at the offshore subsurface levels than that described by Allen in 1922. It is very probable that the production of oceanic forms is less influenced by proximity to land than that of the neritic forms; furthermore, an increased upwelling, by bringing up oceanic water which had not supported phytoplankton for some considerable time, being below the photic zone, would lead to profuse development of oceanic forms. Then again the effect of land-derived materials, at any rate of matter in solution, would appear to be mostly confined to the surface, even for some distance from shore, for the action of upwelling results in carrying out the surface waters. At all events, in the presence of marked differences in the plankton between two years, one may be prepared for differences in distribution of the nature we have just described.

COMPARATIVE PRODUCTIVITY OF SURFACE AND OTHER LEVELS

At both stations the number of diatoms falls off markedly at a depth of ten meters, increasing again at twenty meters to an amount comparable to that of the surface, and increasing still further at thirty meters to an amount several times that of the surface layer. At forty meters the quantity decreases somewhat, rising again at fifty meters. In the case of station 1, ten miles offshore, the amount at fifty meters reaches a maximum for all levels. At sixty meters the amount falls off again, notably so in the case of station 1, though at both stations

the sixty-meter level is more productive than the surface. But since the number of hauls at the greater depths was small it is not proposed to attempt generalizations of too wide an order. The conclusion best supported would seem to be that the greatest production of diatoms takes place between twenty-five and fifty-five meters, and that the upper twenty meters of water are comparatively poor. The case of the dinoflagellates, however, is very different, the surface layers being by far the most important region of production.

TABLE COMPARING THE NUMBER OF DIATOMS AND DINOFLAGELLATES FOUND AT THE VARIOUS LEVELS

Average numbers are given

	Surface	10 m.	20 m.	30 m.	40 m.	50 m.	60 m.
Station 1	13,292	291	11,118	80,231	62,755	115,428	18,866 diatoms
(10 miles out)	1,832	96	471	1,303	440	675	140 dinoflagellates
Station 2	19,336	4,222	11,085	64,109	24,906	32,545	27,954 diatoms
(5 miles out)	9,913	277	422	529	377	164	62 dinoflagellates

Only five hauls were made at depths greater than sixty meters. One from sixty-five meters at station 2 on August 4 contained 127,032 diatoms per liter, mainly *Chaetoceras criophilum* Castracane and *Rhizosolenia semispina* Hensen. It is possible that this haul was taken during the incidence of a swarm at that level (at sixty meters the number was 54,000) and may not approximate to an average. From sixty-nine meters, station K2,* October 6, an amount of plankton was found approximating to the average for the surface. Two hauls at about the same date from eighty meters at station 1 showed considerably less than half the average surface amounts. One haul at one hundred and twenty meters, September 23, contained only traces of plankton. The probability is that below sixty meters no very heavy production takes place.

* See figure 1 for the positions of all stations referred to in text.

QUESTION OF MUTUAL EXCLUSION OF DIATOMS AND DINOFLAGELLATES

Allen (1922), dealing with surface catches of plankton at La Jolla, has called attention to the possibility that diatoms and dinoflagellates may tend to be mutually exclusive in their maxima of production. The evidence, however, as he points out, does not yet warrant a definite conclusion upon this point. It has been pointed out in this paper that in our material the dinoflagellates were found to be most abundant at the surface while the diatoms reached their maximum development between twenty-five and fifty-five meters. In general, a

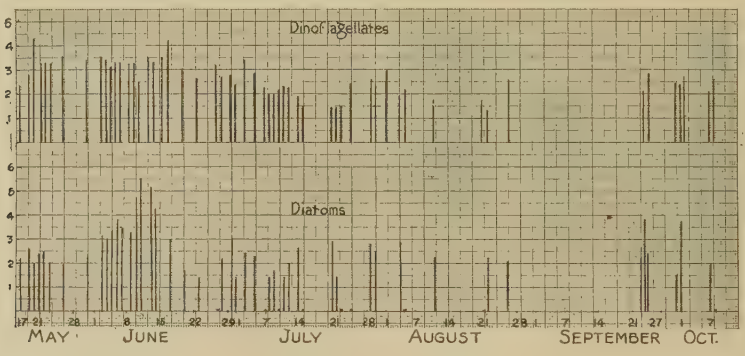

Fig. 2. Graphical representation of the abundance of diatoms and dinoflagellates at the surface level of station 1 throughout the period. The black columns are proportional in height to the logarithms of the number of cells per liter.

high production of diatoms at the surface was associated with a high production of dinoflagellates. Thus, between May 5 and June 20 there occurred a period of abundance, revealed at both stations and participated in by both groups of organisms (figs. 2, 3). From the latter date until August 26 production with minor fluctuations was fairly uniform at the surface with a slight falling off toward the end of the period. When boat operations, after a month's pause, were resumed at the stations on September 23 and continued till October 8, evidence of a new pulse appeared, though this was not so marked as the earlier one. This latter pulse was shared by both groups. Thus it appears that if the pulses are due to the advent of food material, as is probably the case, both groups can take advantage together of the favorable conditions. Although the actual culminating points of the two pulses do not always exactly coincide, there is no evidence that could lead one to say whether the pulse in one group tends to precede or to follow that in the other. The diatom pulse seems

to be sharper than that of the dinoflagellates, the curve of the former rising more steeply and presenting a more strongly marked climax. The diatoms also exhibit greater fluctuations in abundance than the dinoflagellates, over both long and short periods of time. The curves of both groups exhibit minor fluctuations superimposed upon the major ones. In connection with the question of exclusion it is rather interesting to note, as pointed out later on, that the maximum recorded for *Rhizosolenia semispina* Hensen occurs at the same time and in the same place as that for *Peridinium divergens* Ehrenberg. There seems indeed to be little evidence that the two groups are in any degree exclusive of each other.

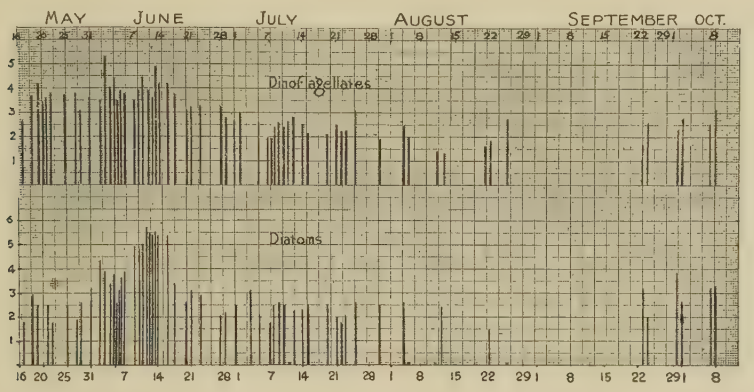

Fig. 3. Graphical representation, as in figure 2, of the abundance of diatoms and dinoflagellates for the surface at station 2.

SPECIAL SERIES

In addition to the regular boat work done at the established stations 1 and 2, on certain days special series of hauls were taken at positions or stations a relatively short distance apart along given courses in the vicinity. These stations are shown in figure 1. The main advantage of these series of observations is that they give a connected picture of the abundance of plankton over a considerable stretch of sea at one time.

Series C

The greater productivity of the surface layers of the inshore region is again borne out by a comparison of the catches in this series, taken on May 8 on a line running northwest from San Diego Bay to station 2. Over 100,000 diatoms per liter were encountered near the mouth of San Diego Bay, a large, nearly land-locked body of

water surrounded by a populous region, which is a center of marked plankton production. The number of cells falls at the whistling buoy and remains at several thousand per liter off La Jolla, falling, in the case of diatoms to mere traces at C6 and station 2. The dinoflagellates did not show such marked fluctuations, remaining between 2,000 and 16,000.

Series D

Series D began on June 4 at 5:18 A.M., at the pier amid an abundance of *Prorocentrum micans* Ehrenberg and traces only of diatoms. All the catches were made at the surface. At about two and one-half miles from shore the diatoms had increased some forty-fold and the dinoflagellates had dropped to about half in number. The diatoms throughout consisted mainly of *Chaetoceras* (*Hyalochaete*) sp. At five miles the diatoms had markedly dropped, suggesting that a local swarm had been encountered. At seven to nine miles another swarm of diatoms (*Chaetoceras*), far more dense, was crossed, while the dinoflagellates also increased somewhat. At station 1 both groups were declining. On the return journey a series of hauls was taken between station 2 and shore, in the same positions as the first five hauls going out were taken, but about four hours later. We found that the numbers of dinoflagellates between station 2 and shore had greatly increased, the increase a mile from the shore being as much as from 9,000 to 54,000 cells per liter. It is very unlikely that these increases were due to reproduction during the period of time from the first to the second visit. The most probable interpretation is that we were dealing with the drifting in of a swarm of planktonic organisms, brought about by the long-shore or tidal currents. An ascent of dinoflagellates to the surface may have been brought about by an increasing smoothness of the surface of the sea, as in the three days previous the sea had been gradually becoming more quiet. This explanation is not very probable, however, for we have generally found that the dinoflagellates are not very numerous at any distance below the surface. Another interesting point brought out by the series is the very sharp increase in diatoms from three and one-half to three miles from shore (from 100 to 32,000 per liter). This supports further the evidence of Allen (1923) that "there is not the slightest indication of uniform distribution over a wide area."

Series E

On June 11, a week later, a similar series of surface catches was taken over the same course, the hauls being taken as before at intervals of about one mile. On this occasion also we found that the number of diatoms was low near shore, with a decided increase less than one mile out. The dinoflagellates as before were considerably more numerous inshore on the return journey than they were on going out. The principal diatoms were *Chaetoceras* (*Hyalochaete*) sp.; the dinoflagellates, *Prorocentrum micans* Ehrenberg, *Peridinium* sp., and *Ceratium* sp.

Series F

On June 23 a series of surface hauls began at the pier of the Institution, running westward at intervals of about two and one-half miles to station 1, ten miles out, and continuing to San Diego Bay. In these hauls the numbers of dinoflagellates were low, averaging about 1,500 per liter. The variations in diatoms were considerable and significant. They are illustrated in figure 4 by black circles, the area of the circle being directly proportional to the number of diatoms per liter. The relatively immense production in San Diego Bay is shown, the influence of this prolific area apparently extending some distance out. On the line from station 1 to the whistling buoy an increase occurs about midway, corroborating the conclusion reached elsewhere that the most highly productive surface area really lies a little beyond station 2, i.e., about seven miles out. Several species of diatoms were strongly predominant at different stations in this series. Outside of San Diego Bay the assemblage *Chaetoceras* (*Hyalochaete*) sp. was most common, with *Rhizosolenia semispina* Hensen and *R. alata* Brightwell becoming increasingly important as the mouth of the bay was approached, until, between the whistling buoy and the narrow mouth of the bay, *Rhizosolenia* passed *Chaetoceras* in numbers. Within the bay a dense swarm of *Eucampia zoodiacus* Ehrenberg was encountered at stations 16 and 17; and still closer in at stations 18, 19, and 20, *Asterionella japonica* Cleve came sharply into first place. At these innermost stations *Eucampia, Chaetoceras,* and *Rhizosolenia* were still abundantly productive. These heavy catches were characterized by a great variety of species, over thirty species being identified in this place. This is in accordance with Allen's conclusion (1920), namely, that increase in one form was associated usually with increase in many forms. While presenting evidence in support of this conclusion, we are of the opinion that it ought not to be taken

as a generalization, as we also found conditions elsewhere comparable to those reported by Fish (1925), where increased production in one form was associated with the suppression of most of the other forms. The point will be referred to later on.

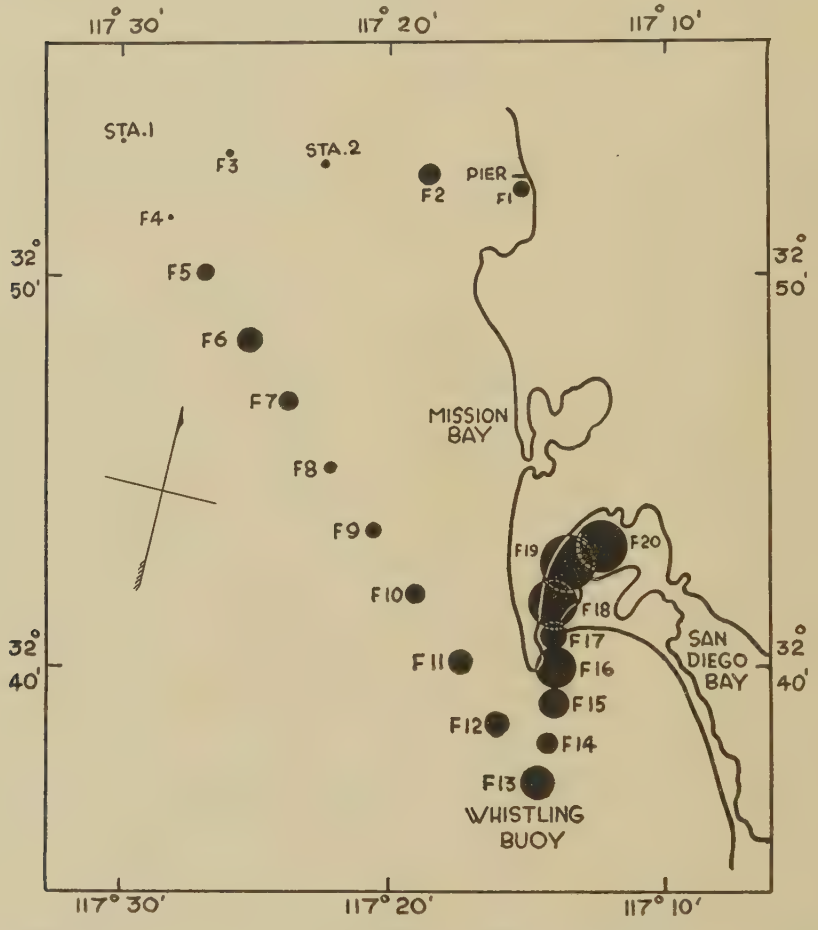

Fig. 4. Representation of the abundance of diatoms over series F on June 23. The black circles are proportional in area to the numbers of cells per liter. F13 = 22,000.

Series J

Series J began opposite the main portion of the water front of San Diego, with catches made at intervals of two miles. The productivity at this time, September 9, was very low at all stations including the subsurface levels which were investigated in the case of the whistling buoy station. Only in one locality, two miles north of the whistling buoy, did the number of diatoms exceed 3,000 cells per

liter. At this time much bottom débris was to be found at the surface, and tychopelagic forms were conspicuous, indicating an unusual amount of disturbance by winds or currents.

A matter which would appear to deserve serious consideration among the factors governing distribution is that of the effects of coastal currents, not only along the shore line, where, alone, measurements are possible, but at places farther out. In the shore region of the locality there is evidence of prevailing currents of considerable magnitude in opposite directions. The extensive sand-bar of San Diego Bay (fig. 1), whose extremity is pointed up-coast, indicates a

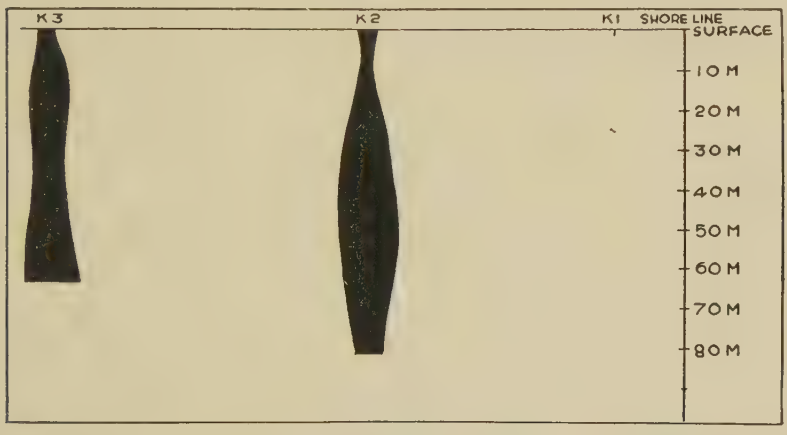

Fig. 5. Representation of bathymetrical distribution of diatoms at stations K1, K2, K3, on October 6. The width of the black area is proportional to the square root of the number of cells per liter. K2, 50 m. = 33,600. At K1 only the surface was investigated and diatoms were not present in large enough numbers to be recorded.

prevailing current to the north, while the bar of Mission Bay, whose extremity is pointed down-coast, indicates a prevailing current to the south. These currents may be influential in determining the distribution of land-derived material even at a distance of some miles from the coast. This influence is a matter for future investigation.

Series K

Series K comprised sixteen catches made on October 6, at the surface in the case of station K1, close to the shore, and at various levels at K2 and K3, one and two miles from shore, respectively. The distribution of diatoms is shown in the form of a vertical section in figure 5. The dinoflagellates were present in small amounts, less than 1,000 cells per liter; they are therefore omitted from the graph. No diatoms were found (in micro-enumeration) at K1. Again we

observe the fact that the production of diatoms was markedly deficient close to the shore, and increased successively at one mile and two miles from shore. Only traces of diatoms were found at K2, ten meters, whereas 18,000 per liter were found at K3, ten meters. The largest number of diatoms found was 33,656 at K2, fifty meters. The most prominent forms were *Chaetoceras* (*Hyalochaete*) sp., *Rhizosolenia semispina* Hensen, *Bacteriastrum varians* Lauder, *B. elongatum* Cleve, and *Nitzschia seriata* Cleve.

SPECIES OF DIATOMS MOST ABUNDANT

Asterionella japonica Cleve

This species was recorded from only fourteen catches, one of which was from a considerable depth (forty meters); the remainder were all surface catches. It is interesting that in the three heavy surface catches taken inside of San Diego Bay it was the preponderating species, averaging for the three catches 50,000 cells per liter. Elsewhere it was mostly confined to the stations near land. Its southern temperate, neritic nature seems to be illustrated by its high development in a land-locked, sun-warmed basin; the temperature at the stations where it was found in such abundance ranged from 17.77° to 19.51° C., while for several miles outside of San Diego Bay the temperature was between 16° and 17° C. The maximum abundance was: F20, surface, June 23, 72,000 per liter, temperature 19.51° C., pH 8.30.

Bacteriastrum varians Lauder

This form was not very numerous until August 6, when it attained 8,000 per liter at station 1, forty meters. On the whole it was more abundant at the inner stations. During most of September no work was done at sea, but a series of hauls with the Kofoid bucket was made at the Institution's mooring, about 2,000 feet from shore. From September 8 to 23 *Bacteriastrum varians* entered a period of moderate productivity, frequently exceeding 20,000 per liter at all levels, though in this work the greatest depth examined was only fifteen meters. The evidence is that the optimum conditions for the species lie a moderate distance below the surface. Maximum recorded: 56,000 per liter, September 12, at 7.5 meters. No other data are available.

Chaetoceras criophilum Castracane

The oceanic character of this form is borne out by its distribution among the catches, where it is only sparingly represented (less than 100 per liter). It is often entirely absent from the catches taken within four miles of land and is not recorded from San Diego Bay. It attained its maximum production at the ten-mile station on July 30: 240,000 per liter at forty meters. At fifty meters in the same place 151,000 were estimated. At sixty meters the numbers were reduced. At the five-mile station it attained its maximum on the same date, 58,000 at fifty meters; on August 11, 55,000 at sixty meters. The fluctuations in number were most pronounced at station 2. The evidence suggests that the optimum conditions lie a considerable distance below the surface, probably between forty and fifty meters. In only one instance was it represented by more than 1,000 cells per liter at the surface. The variety *volans* was abundant. A marked production of *Chaetoceras criophilum* was usually associated with abundance of the subgenus *Hyalochaete.*

Chaetoceras (Hyalochaete) sp.

To identify the individual species of the subgenus *Hyalochaete* is a matter of unusual difficulty, as often the terminal setae and the resting spores are not present. For the purpose of micro-enumeration it was usually necessary to place all of these very minute forms together under the designation given above. The principal forms which composed this assemblage were *Chaetoceras decipiens* Cleve, *C. compressum* Cleve, *C. didymum* Ehrenberg, *C. constrictum* Gran, *C. pelagicum* Cleve, *C. difficile* Cleve, *C. diversum* Cleve, *C. furca* Cleve, *C. subtile* Cleve, *C. pseudocrinitus* Ostenfeld, *C. curvisetum* Cleve, *C. debile* Cleve, *C. scolopendra* Cleve. Further data regarding the occurrence of these forms individually, are filed at the Scripps Institution; space does not permit the publishing of all the figures at present.

Considering the surface catches at stations 1 and 2, we find a pulse of *Chaetoceras* at each during the second week in June. Station 2 was more productive, with a maximum of 459,000 on June 11 (18.62° C., pH 8.48); maximum at station 1, 240,000, June 13 (18.43° C., pH 8.44). The production at this period is illustrated further by series D and E. The numbers were very low close inshore, increasing many times farther out, and it is to be noted that the highest recorded figure of all was reached seven miles from shore, that is, between the two

stations. This was 549,000 at station E8, June 11 (18.57° C., pH 8.45). The dominant form was *C. compressum.* The evidence from series F, a fortnight later, also indicates that the area of greatest productivity is about seven miles from shore. Figure 4, showing the totals in series F, gives an approximate representation of *Chaetoceras* sp. alone except that the latter fell off inside of San Diego Bay. In series J the group was insignificant and also at the mooring on October 3. At the mooring from August 26 to September 23 very high productivity of the assemblage was found, 1,308,160 cells per liter occurring on September 12 at fifteen meters (no other data available). From the end of June till August 26 only small numbers of *Chaetoceras* sp. were found at stations 1 and 2. After that the boat work was suspended for a month and what the conditions were in the meantime are not known. A study of the counts makes it appear that the most favorable levels for the assemblage are at the surface and at a depth of from twenty-five to fifty meters. It has not been possible to analyze the distribution of the individual species as closely as could be desired owing to the difficulties of identification previously referred to. Moreover, no catches were made from the subsurface levels before June 27.

Dactyliosolen tenuis (Cleve.)

Only one pulse of this form was observed (see p. 96). Over the whole of the period *D. tenuis* is represented sparingly, occurring most frequently at depths of from thirty to sixty meters. Although this is a neritic form, it is interesting to note that it is not recorded from San Diego Bay during the period of high productivity. The pulse of *Dactyliosolen tenuis* July 10–14 is figured in the accompanying table. At this time it was absent from the surface layers with the exception

Table of the Pulse of Dactyliosolen tenuis During the Second Week in July

	Station 2 (5 miles out)					Station 1 (10 miles out)				
	July 10	July 11	July 12	July 13	July 14	July 10	July 11	July 12	July 13	July 14
Surface	0*	0	0	.....	0	0	0	0	.....	28
10 meters	.....	.....	33,040	.....	84	.....	.....	0	.....	980
20 meters	0	504	2,352	.....	1,904	0	0	56	.....	168
30 meters	1,456	1,232	18,200	.....	2,660	420	5,180	756	.....	3,200
35 meters	.....	.....	1,316	.....	.....	.....	.....	1,700	.....	.....
40 meters	.....	.....	224	.....	84	.....	.....	980	.....	1,092
50 meters	.....	.....	168	.....	.....	.....	.....	300	.....	.....

* The blanks in the table indicate that no catch was made at the particular depth.

of traces at station 1 on July 14, but was present in abundance at ten meters at station 2 on July 12. Two days later it had almost vanished from the ten-meter level at station 2, though by then it had come into prominence at station 1. In the case of both stations the species diminished somewhat at the twenty-meter level, reaching a second maximum at thirty meters. It was still represented in moderate amount at fifty meters. The maximum recorded was at station 2, ten meters, July 12, temperature 19.08° C., pH 8.46.

Eucampia zoodiacus Ehrenberg

Eucampia zoodiacus, a neritic form, was more abundant at station 2 than at station 1 for all levels. It was recorded in eighty-two catches, often in small numbers, though these small numbers at one station were usually consistently associated with small numbers at the other stations on the same date. Over a number of intervening periods the species is not recorded at all. It attained its maximum on July 3, station 2, where its bathymetric distribution was as follows: Surface, absent or nearly so; 20 m., 1,568; 30 m., 29,000; 40 m., 33,000. At station 1 the corresponding figures were: surface, absent or nearly so; 20 m., 224; 30 m., 980; 40 m., 1,500.

The species was well represented in San Diego Bay reaching 13,000 per liter at the surface, station F16. It was abundant at the mooring, reaching 17,000 at fifteen meters, September 11. It appears in general to be most abundant below thirty meters. Maximum recorded 33,000 per liter, July 3, station 2, forty meters, 10.65° C., pH 8.10.

Leptocylindrus danicus Cleve

This species was present in 34 catches, and was more numerous at station 2 than station 1. Maximum recorded: station 2, 30 meters, July 3, 9,000 per liter, 11.45° C., pH 8.19.

Rhizosolenia semispina Hensen

This boreal arctic oceanic species was the most important constituent of the phytoplankton, being found in a very high percentage of the catches. On account of its large size, by far the greatest amount of the vegetable matter produced in the sea during the period must have been locked up in *Rhizosolenia.* In the distribution of this species we find substantially the conditions which have been described for the phytoplankton as a whole, namely, that the inshore surface levels

(station 2) contained slightly greater numbers than the offshore surface levels (station 1). At a depth of twenty meters station 1 is slightly more prolific, and below that the offshore depths are more productive than the inshore, with the exception of the sixty-meter level, where, however, the number of catches was hardly sufficient to establish a comparison.

Comparison of the Average Numbers

Station	Depth in meters	Number per liter
1	Surface	200
2	Surface	300
1	10	150
	20	ca. 11,000
2	10	ca. 800
	20	ca. 9,000
1	25	ca. 130,000
	30	ca. 76,000
2	25	ca. 64,000
	30	ca. 30,000
1	35	60,000
	40	35,000
	50	27,000
	60	6,500
2	35	20,000
	40	27,000
	50	8,000
	60	13,000

It will thus be seen that the features of the distribution of the plankton as a whole can largely be accounted for by the distribution of *Rhizosolenia semispina,* for this form was the dominant one, and, as in the case of *Chaetoceras* (*Hyalochaete*) sp. in relation to the greater part of series F, the totals of all the species will be determined chiefly by those of the dominant form. Indeed, the fact of the great abundance of *Rhizosolenia semispina* in the coastal waters in 1924 may be adequate to account for the differences in distribution of the phytoplankton as a whole from that observed by Allen in 1922. In 1922, according to Allen, *Rhizosolenia* was not present in any considerable numbers. The year 1924 was, indeed, a *Rhizosolenia semispina* year for the region. The question arises whether an oceanic form would be influenced to the same degree by proximity to land as the neritic forms. The former depends upon the material normally available in oceanic waters, whereas the latter are not found far from land and are dependent largely upon land-derived materials. Thus the surface catches, in which neritic forms predominated, would be more influenced by land drainage at station 2 than at station 1, hence the greater productiveness of station 2 at the surface. But at the

subsurface levels where *Rhizosolenia* was found in such abundance, it is very doubtful whether land-derived material would play much part, because, as we have pointed out, the temperature records of McEwen indicate that the amount of upwelling in 1924 was above the average. The effect of such upwelling is to carry the warmer and lighter inshore water as a thin film over the deeper and colder layers upwelling from below the photic zone. Such layers of deep oceanic water have not supported phytoplankton for a long period; they are therefore presumably refilled with food substances after their long sojourn in the subphotic regions amid the purely animal life that exists there. Thus they are ready for the active production of oceanic phytoplankton when they are drawn up into the photic zone and seeded. Their phosphate content, for example, is far higher than that of the surface waters, and they are also richer in carbon dioxide. It may therefore well be that the differences in plankton distribution between 1922 and 1924 are due to the variation in fundamental physical conditions, namely, the greater amount of upwelling in 1924.

Adaptability of Oceanic Species

The question may now be considered, whether an oceanic form can profit by neritic conditions in the way that the neritic forms can increase during periods of pronounced land drainage. The only available evidence concerning this question is incidental to observations made for other purposes. It is therefore purely suggestive. Allen found *Chaetoceras criophilum* Castracane, another oceanic form, in great quantity at the mouth of San Diego Bay in 1922. Fish found *Rhizosolenia semispina* Hensen present in large quantities in Buzzard's Bay and Vineyard Sound, Woods Hole, in 1922 under highly neritic conditions. These observations suggest that oceanic forms may profit by inshore conditions in the same way as do neritic forms. Fish, however, is inclined to believe that ocean currents may have been responsible for the great influx of *Rhizosolenia* into the waters he investigated. We are able to confirm Fish's finding that the neritic species may play only a small part in production in the presence of a single dominant oceanic form, *a fortiori,* when it is borne in mind that the dominance of *Rhizosolenia semispina* is more significant than appears under the conventional method of enumeration where equal status is given to all forms irrespective of size. One individual cell of *Rhizosolenia semispina* is the equal of large numbers of cells of the small *Chaetoceras* (*Hyalochaete*) sp., e.g., *Chaetoceras scolopendra.* The catches rich in *R. semispina* usually contained moderate or large amounts of *Chaetoceras criophilum* Castracane, *Thalassiothrix longissima* Cleve and Grunow, and *Nitzschia seriata* Cleve, all boreal arctic

oceanic forms. It is interesting to note the tendency to the elongated form in such assemblages, the long thick chromatophore-bearing spines of *C. criophilum* simulating the body form of the other types. *R. semispina* attained its recorded maximum on July 7, station 1, 30 m., 750,000 cells per liter, temperature *ca.* 11.49° C., pH 8.27. (See also *Peridinium divergens.*)

SPECIES OF DINOFLAGELLATES

The dinoflagellates were less numerous than the diatoms. The most highly productive form was *Prorocentrum micans* Ehrenberg, with the genera *Peridinium, Ceratium,* and *Dinophysis* almost constantly represented.

Peridinium spp.

This assemblage was made up mainly of *P. divergens* Ehrenberg and *P. minutum* Kofoid. Station 2 was more productive than station 1, and the surface was the most productive level for the greater part of the period. On July 7, at station 1, thirty meters, a swarm of *P. divergens* was encountered—11,000 per liter. It was rather exceptional to find this development at so great a depth, also the swarm was associated with a dense development of *Rhizosolenia semispina* (750,000 per liter). Incidentally, these are the greatest recorded maxima for both these forms (see above for physical and chemical data). What caused this unusual development cannot be answered. Still more remarkable is the fact that the swarm was highly circumscribed, there being no evidence of large production at the neighboring levels. A swarm of *P. minutum* was encountered at the surface two to four miles from shore on June 11, station E13, 26,000 per liter.

Ceratium spp.

The most common species were *C. tripos* (O. F. Müller) Nitsch., *C. fusus* (Ehrenberg) Claparede Laachmann, *C. furca* (Ehrenberg) Claparede Laachmann, *C. kofoidii* Jörgensen, and *C. azoricum* Cleve. The counts show that this genus, like the other dinoflagellates found, is mainly confined to the surface layers. Station 2 was several times more productive than station 1. Maximum recorded: 15,000 per liter, station D15, surface, June 4, 19.57° C., pH 8.64.

Dinophysis spp.

Dinophysis acuminanta Claparede Laachmann, *D. homunculus* Stein, and *D. ovum Schütt,* occurred regularly, though sparingly, at all levels.

TEMPERATURES

Figures 6, 7

The average temperatures for the various depths at stations 1 and 2 have been determined for fortnightly periods during the time of boat operations. At the surface the highest temperature was reached at both stations in July (station 1, average for second half of July, 20.38° C.; station 2, 20.32° C.). In May, station 1 was slightly warmer than station 2 at the surface. From June onward station 1

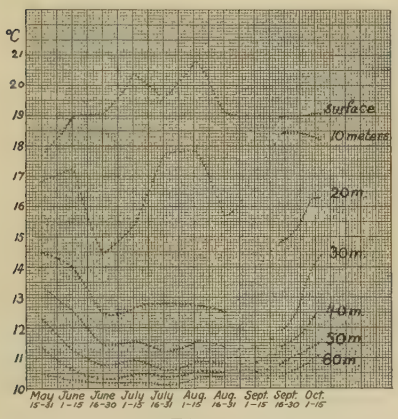

Fig. 6

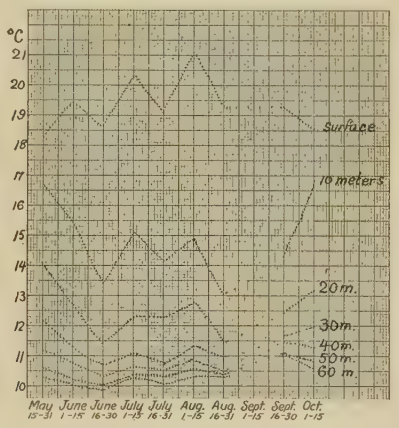

Fig. 7

Fig. 6. Graphs of fortnightly averages of temperature over the period at surface and subsurface levels of station 1. During one fortnightly period no boat work was done, and hence a hiatus.

Fig. 7. Temperature graph for station 2.

was slightly warmer at the surface than station 2. The same differences usually apply at the subsurface depths, station 1 being almost invariably warmer than station 2, sometimes by as much as 1° C. Allen, studying the 1922 catches, noted that a pulse in production was coincident with a drop in surface temperature. This happened in June, and the present series shows almost exactly the same coincidence. The plankton pulses at the middle of June came during a period of falling temperature, which culminated during the second half of June and was apparent at all levels. This may have marked a period of strong upwelling which drove to the surface masses of water previously devoid of phytoplankton and unexhausted of the constituents that favor its development. The neritic forms appear to have profited equally from this advent of fertile oceanic water. The interpretation of the relationship of the fall of temperature to

increased production given above is somewhat different from Allen's suggestion that upwelling might force the main diatom population to the surface. There is evidence here that the main diatom population is still considerably below the surface, and that it is of a more oceanic character than the surface plankton.

PHOSPHATE

The data on phosphates in milligrams per liter, obtained by Moberg from water samples taken at the same time as the plankton hauls, have been studied in relation to the abundance of phytoplankton. Figure 8 is a graph of the amounts of phosphate at the surface for stations 1 and 2. We note that the amount is greater during the period of high productivity in June. The phosphate curves for the two stations are

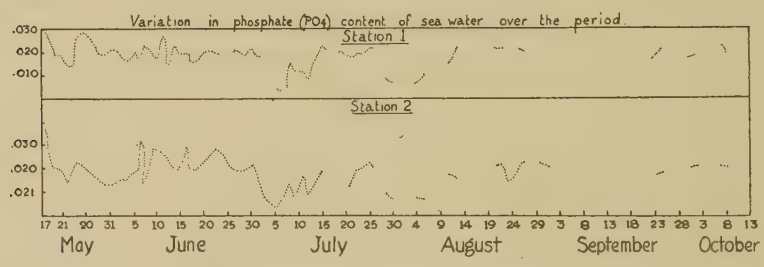

Fig. 8. Graph to illustrate the amount of phosphate present in the surface water at stations 1 and 2.

in fairly close agreement as regards their major fluctuations. Station 1, however, seems to be slightly superior to station 2. A good correlation between PO_4 at the surface and plankton production is furnished by the figures for series F. The amounts, in thousandths of a milligram for the series F1, F2, etc., are 19, 23, 19, 19, 22, 22, 24, 20, 20, 21, 21, 25, 24, 23, 24, 23, 27, 46, 49, 51 (compare with fig. 4 illustrating abundance of plankton). Over series J, which was very low in plankton, no corresponding decrease in phosphate was to be observed. The amount of phosphate increases with depth. Between 200 and 300 meters the amount is usually about .170 milligrams per liter. If the number of meters in the depth is used to denote thousandths of milligrams the result will usually be within twenty or thirty of the amount of phosphate (up to 200 meters). A comparison of the variations in phosphate has been made with the amount of plankton at a depth of thirty meters below the surface; a correlation is exhibited similar to that at the surface though not so close. The

data for the comparisons at depths are not sufficiently extensive to permit us to pursue the question very far.

It seems probable that the variations both in temperature and in phosphate are expressions of the degree of upwelling, the former being inverse to the latter. The lower temperature of station 2, as compared to station 1, can be interpreted from the known fact that the bottom water creeps up to the littoral zone and then flows slowly out to sea. Thus the water at the distant station has been longer at the surface than the water at the nearer station and has had a longer time in which to absorb solar radiation. In the region under discussion the summer rainfall is very slight. The records for San Diego show that no rain fell during the period. In April, 0.77 inch was recorded. Since the series did not begin till after the middle of May, the April rainfall could have had but little influence. Again, but little of the rain which falls in summer reaches the sea, since most of it is immediately absorbed into the ground or is evaporated. Of course there is some slight drainage into the sea from the villages along the coast, and considerable drainage from the city of San Diego into San Diego Bay. This is an artificial influx of water, bearing material suitable for the support of plankton, hence the heavy production in the bay. Were it not for this drainage from the city of San Diego, it is to be questioned whether the bay would be any more productive during the summer than the open sea. Allen found that Mission Bay, which is not surrounded by a populous area, was less productive than the open sea. These bays, did they receive flowing rivers as in a country of higher rainfall, would certainly be highly productive irrespective of whether cities discharged their sewage into them. But the summers of southern California are a period of almost unbroken drought, and normally, during the summer, but little land material is supplied for the support of plankton. It is therefore to be considered whether the normal superiority of the surface waters of station 2 over station 1 is necessarily to be interpreted as an expression of proximity to the source of land material. The facts of upwelling offer an explanation equally plausible, for, as we have just pointed out, the upwelling water rises to the surface close to the shore and flows out to sea. Thus the nearer water is fresh from the subphotic zone, it becomes seeded, and some distance from the coast it will produce an abundance of plankton. Then exhaustion sets in, and at station 1 signs of depletion are to be observed. All this can happen in the complete absence of land drainage, which is the condition so nearly approached.

SUMMARY

The paper presents an analysis and discussion of marine phytoplankton collected, during the summer months of 1924, off the coast of San Diego County, California. Collections were made at the surface and at known depths by means of the Kofoid bucket. It is found that the production of diatoms at the surface is low inshore, increasing strongly in a zone from three to seven miles from land, and falling off at ten miles, the greatest distance investigated. At a depth of twenty meters the falling off with increased distance from the coast is not apparent; at depths greater than this there is an increase from shore to ten miles. The most abundant collections were made at depths between twenty-five and fifty meters. A comparison with the conditions found in previous years is made, followed by a discussion on the distribution in relation to upwelling, which was above the average in 1924. The plankton in 1924 is marked by the dominance of the boreal arctic oceanic form *Rhizosolenia semispina* Hensen, which has not been recorded as dominant in previous years. It is possible that the environmental requirements of this form may account for the fact that the deeper waters offshore were more prolific than the waters inshore, in contrast to previous years, when increasing distance from shore was marked by a falling off at all levels.

Dinoflagellates were most abundant close inshore at depths between ten meters and the surface. A study of the relationship of the incidences of high production of diatoms and of dinoflagellates does not indicate that the two groups tend to be mutually exclusive.

The main production of phytoplankton occurred at a period of lowered temperature, exhibited at all levels. The interpretation is that upwelling was marked then, bringing up water into the photic zone that had not supported phytoplankton for a long time and which was, when seeded, chemically capable of supporting a heavy phytoplankton. Other data are discussed and interpreted on the basis of upwelling; for example, it is pointed out that in this region of summer drought there can have been no normal land drainage (the drainage from towns, particularly San Diego is discussed separately) and that the superiority of the inshore surface layers can be accounted for on the basis of upwelling. The latter thus simulates conditions of food supply which would obtain in the presence of flowing rivers and abundant land drainage. A discussion of the most prominent individual species is presented. A series of hauls taken from time to time at short distances apart shows that there is great variation in

the plankton at the same time in different parts of a small area, and at the same place within a short period of time. This is explained as being caused by the action of the currents. Reference is made to physical and chemical environmental factors.

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